



**University of  
Zurich**<sup>UZH</sup>

**Zurich Open Repository and  
Archive**

University of Zurich  
University Library  
Strickhofstrasse 39  
CH-8057 Zurich  
[www.zora.uzh.ch](http://www.zora.uzh.ch)

---

Year: 2019

---

## **Response to Comment on “Impacts of species richness on productivity in a large-scale subtropical forest experiment”**

Bruehlheide, Helge ; Chen, Yuxin ; Huang, Yuanyuan ; Ma, Keping ; Niklaus, Pascal A ; Schmid, Bernhard

Abstract: Yang et al. have raised criticism that the results reported by us would not be relevant for natural forests. We argue that productivity is positively related to species richness also in subtropical natural forests, and that both the species pools and the range of tree species richness used in our experiment are representative of many natural forests of this biome.

DOI: <https://doi.org/10.1126/science.aav9863>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-168739>

Journal Article

Accepted Version

Originally published at:

Bruehlheide, Helge; Chen, Yuxin; Huang, Yuanyuan; Ma, Keping; Niklaus, Pascal A; Schmid, Bernhard (2019). Response to Comment on “Impacts of species richness on productivity in a large-scale subtropical forest experiment”. *Science*, 363(6423):eaav9863.

DOI: <https://doi.org/10.1126/science.aav9863>

## Response to Comment on “Impacts of species richness on productivity in a large-scale subtropical forest experiment”

Helge Bruelheide<sup>1,2</sup>, Yuxin Chen<sup>3</sup>, Yuanyuan Huang<sup>3</sup>, Keping Ma<sup>4</sup>, Pascal A. Niklaus<sup>3</sup>, Bernhard Schmid<sup>3</sup>

1 Institute of Biology / Geobotany, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany

2 German Centre for Integrative Biodiversity Research (iDiv) Halle–Jena–Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

3 Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

4 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.

### Abstract:

Yang et al. have raised criticism that the results reported by us would not be relevant for natural forests. We argue that productivity is positively related to species richness also in subtropical natural forests and that both the species pools and the range in tree species richness used in our experiment are representative of many natural forests of this biome.

Cautiously extrapolating the losses in productivity observed in our experiment to the global scale, we argued that a decline in species richness by 10% might result in a reduction of productivity by 2.7% **(1)**. This productivity decline was in a similar range as the one predicted by Liang et al. **(2)** based on a global analysis of forest inventory plots. Specifically, our own prediction is based on averaging the wood volume increment from 2016 to 2017 at the planted species richness levels (1, 2, 4, 8, 16) and estimating the productivity decrease expected under a loss of 10% of the species. This loss was determined from fitted linear models and amounted to 3.8, 3.0, 2.5, 2.2 and 1.9%, respectively, averaging 2.7% across these richness levels.

In our experiment, a linear fit of productivity to the logarithm of species richness best described the data. Therefore, the absolute productivity loss per halving of species numbers was constant across the richness gradient, with constant absolute amounts translating into decreasing percent amounts at higher richness levels. In their study, Liang et al. **(2)** found that a log-log relationship fitted their data better, resulting in a model that implied a constant proportional productivity loss when a given fraction of species was lost. Contradicting both of these models, Yang et al. **(3)** now argue that the richness-productivity relationship is saturating, and that effects would therefore vanish to zero at our observed maximum species richness and beyond. Yang et al. even argue that productivity would be stable unless 50% or more of species were lost from the full species set. This conclusion clearly contradicts our finding of a linear productivity decrease with a logarithmic decrease in species richness.

In parallel to the experiment we reported **(1)**, we also analysed the richness–productivity relationship in comparative study plots **(4)** in the Gutianshan National Nature Reserve (Zhejiang

Province) (5, 6). These plots were located 30 km from our experimental site, were of comparable size (i.e. 30 x 30m) (7), and ranged in tree species richness from 3 to 20, far below the average of 27 in Yang et al. These data indicate that the experimental species gradient we implemented is in accordance with diversity levels found in the natural forests of our study region.

We disagree with Yang et al.'s conclusions for further reasons. First, we chose the species for our experiment as representative sample of the regional pool (4). Thus, all species in the experiment co-occur in natural communities, refuting Yang et al.'s argument of having established artificial species mixtures. Second, even a richness level of 27 species is close to the maximum richness of 24 in our experiment. Because of the species-area relationship (SAR), richness in natural communities increases with plot size [see (8) for SARs for Gutianshan], whereas ecosystem functioning is largely scale-invariant above a minimum size. Results from a 24 ha-plot in Gutianshan (9) showed that this minimum size was about 1 mu (666 m<sup>2</sup>) and that richness-productivity relationships were strongest at plot sizes of 30 m x 30 m and 40 m x 40 m, supporting our decision to focus on that plot size as the relevant ecosystem scale. In fact, many diversity mechanisms operate already at much smaller scales. We showed that 53.5% of the aboveground wood production of a given target tree in our experiment is brought about by the neighbourhood composition of the eight surroundings trees (10)—that is, by effects operating on an area of 15 m<sup>2</sup>. Using the SARs of (8) shows an estimated richness of 3.7 in natural forests at 15 m<sup>2</sup>, which is perfectly covered by the richness gradient in our experiment. Third, measurements from our comparative study plots demonstrate that the richness–productivity relationship in natural forests in the region does not take the form of a saturation curve; instead, there is evidence for a steady linear increase in the observed range (5, 6). Within any given age class of a forest, Liu et al. (6) described increasing aboveground C fluxes and stocks with increasing tree species richness. Fourth, the statement that we did not find a notable change in net biodiversity effects from 8- to 16-species communities is a misinterpretation of our results. The power to detect differences between these two levels in separate analyses excluding all other richness levels is low because of the low number of replicates for these richness levels. The strength of our analysis arises from the entire extinction series. In particular, it allows to generalize beyond analyses that center around just a few species or mixture-polyculture comparisons (11, 12). We have fitted different models and did not find any significant deviations from the trend that a doubling of species richness causes a constant absolute increase in productivity measures. Thus, our analysis indicates that productivity also increased from 8 to 16 species, an increase mainly brought about by increased complementarity effects [figure 2 of (1)]. We cannot see how Yang et al. have arrived at <0.1 % for a 4-year mean net biodiversity effect, using values manually extracted from our figure 2. Of course, we agree that per-species changes in richness lead to a greater loss of ecosystem functions at low than at high diversity. Specifically, our model implies that adding one species to a monoculture increases productivity as much as adding further eight species to an 8-species mixture. This makes our results particularly relevant for forestry, which is based largely on monocultures. In southeastern China, such monocultures dominate the landscape. Thus, the histogram of species richness (figure 1 of Yang et al.) is far from being representative for the forests in that region.

Finally, we fully agree that isolating species richness effects from the confounding factors of climate and soil conditions is very difficult. Actually, this is the main motivation to carry out experiments where species richness levels can be randomly assigned to plots (4). Similarly, our comparative study sites were selected to reflect a gradient in species richness, trying to control for confounding variables (such as forest age (5–7)). The comment of Yang et al. shows how

appropriate it was that we had set up the experiment jointly with a comparative study in natural forests.

1. Y. Huang, Y. Chen, N. Castro-Izaguirre, M. Baruffol, M. Brezzi, A. Lang, Y. Li, W. Härdtle, G. von Oheimb, X. Yang, X. Liu, K. Pei, S. Both, B. Yang, D. Eichenberg, T. Assmann, J. Bauhus, T. Behrens, F. Buscot, X.-Y. Chen, D. Chesters, B.-Y. Ding, W. Durka, A. Erfmeier, J. Fang, M. Fischer, L.-D. Guo, D. Guo, J. L.M. Gutknecht, J.-S. He, C.-L. He, A. Hector, L. Hönl, R.-Y. Hu, A.-M. Klein, P. Kühn, Y. Liang, S. Li, S. Michalski, M. Scherer-Lorenzen, K. Schmidt, T. Scholten, A. Schuldt, X. Shi, M.-Z. Tan, Z. Tang, S. Trogisch, Z. Wang, E. Welk, C. Wirth, T. Wubet, W. Xiang, M. Yu, X.-D. Yu, J. Zhang, S. Zhang, N. Zhang, H.-Z. Zhou, C.-D. Zhu, L. Zhu, H. Bruelheide, K. Ma, P.A. Niklaus, B. Schmid: Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* **362**, 80–83 (2018).
2. Liang, J.J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch, S. de-Miguel, A. Paquette, B. Hérault, M. Scherer-Lorenzen, C. B. Barrett, H. B. Glick, G. M. Hengeveld, G.-J. Nabuurs, S. Pfautsch, H. Viana, A. C. Vibrans, C. Ammer, P. Schall, D. Verbyla, N. Tchebakova, M. Fischer, J. V. Watson, H. Y. H. Chen, X. Lei, M.-J. Schelhaas, H. Lu, D. Gianelle, E. I. Parfenova, C. Salas, E. Lee, B. Lee, H. S. Kim, H. Bruelheide, D. A. Coomes, D. Piotta, T. Sunderland, B. Schmid, S. Gourlet-Fleury, B. Sonké, R. Tavani, J. Zhu, S. Brandl, J. Vayreda, F. Kitahara, E. B. Searle, V. J. Neldner, M. R. Ngugi, C. Baraloto, L. Frizzera, R. Bałazy, J. Oleksyn, T. Zawila-Niedzwiecki, O. Bouriaud, F. Bussotti, L. Finér, B. Jaroszewicz, T. Jucker, F. Valladares, A. M. Jagodzinski, P. L. Peri, C. Gonmadje, W. Marthy, T. O'Brien, E. H. Martin, A. R. Marshall, F. Rovero, R. Bitariho, P. A. Niklaus, P. Alvarez-Loayza, N. Chamuya, R. Valencia, F. Mortier, V. Wortel, N. L. Engone-Obiang, L. V. Ferreira, D. E. Odeke, R. M. Vasquez, S. L. Lewis, and P. B. Reich: Positive biodiversity-productivity relationship predominant in global forests. - *Science* 354: aaf8957 (2016).
3. H. Yang, Z. Guo, X. Chu, R. Man, J. Chen, C. Liu, J. Tao, Y. Jiang, Comment on "Impacts of species richness on productivity in a large-scale subtropical forest experiment". *Science* 636, eaav9117.
4. Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F., Chen, X.-Y., Ding, B.-Y., Durka, W., Erfmeier, A., Gutknecht, J.L.M., Guo, D.L., Guo, L.-D., Härdtle, W., He, J.-S., Klein, A.-M., Kühn, P., Liang, Y., Liu, X.J., Michalski, S., Niklaus, P.A., Pei, K.Q., Scherer-Lorenzen, M., Scholten, T., Schuldt, A., Seidler, G., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wubet, T., Yang, X.F., Yu, M.J., Zhang, S.R., Zhou, H.Z., Fischer, M., Ma, K.P., Schmid, B.: Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. - *Methods in Ecology and Evolution* 5: 74–89 (2014).
5. Baruffol, M., Schmid, B., Bruelheide, H., Chi, X., Hector, A., Ma, K.P., Michalski, S., Tang, X.Y., Niklaus, P.A.: Biodiversity promotes tree growth during succession in subtropical forest. *PLoS ONE* 8: e81246 (2013).
6. Liu, X.J., Trogisch, S., He, J.-S., Niklaus, P.A., Bruelheide, H., Tang, Z.Y., Erfmeier, A., Scherer-Lorenzen, M., Pietsch, K.A., Yang, B., Kühn, P., Scholten, T., Huang, Y.Y., Wang, C., Staab, M., Leppert, K.N., Wirth, C., Schmid, B., Ma, K.P.: Tree species richness increases ecosystem carbon storage in subtropical forests. *Proceedings of the Royal Society Series B* 285: 20181240 (2018).
7. Bruelheide, H., Böhnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X.-Y., Ding, B.-Y., Durka, W., Erfmeier, A., Fischer, M., Geißler, C., Guo, D., Guo, L.-D., Härdtle, W., He, J.-S., Hector, A., Kröber, W., Kühn, P., Lang, A.C., Nadrowski, K., Pei, K.Q., Scherer-Lorenzen, M., Shi, X.Z., Scholten, T., Schuldt, A., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wu, Y.-T., Yang, X.F., Yu, M.J., Zeng, X.Q., Zhang, S.R., Zhou, H.Z., Ma, K.P. & Schmid, B.: Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81, 25-41 (2011).

8. Schuldt, A., Wubet, T., Buscot, F., Staab, M., Assmann, T., Böhnke-Kammerlander, M., Both, S., Erfmeier, A., Klein, A.M., Ma, K.P., Pietsch, K., Schulze, S., Wirth, C., Zhang, J.Y., Zumstein, P. & Bruehlheide, H.: Multitrophic diversity in a biodiverse forest is highly nonlinear across spatial scales. *Nature Communications* 6, 10169 (2015).
9. Lai JS, Mi XC, Ren HB, Ma KP: Species–habitat associations change in a subtropical forest of China. *J. Veg. Sci.* 20, 415–423 (2009).
10. Fichtner, A., Härdtle, W., Li, Y., Bruehlheide, H., Kunz, M. & von Oheimb, G.: Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications* 9, 1144 (2017).
11. Y. Zhang, H.Y.H. Chen, P.B. Reich, Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *J. Ecol.* 100: 742–749 (2012).
12. H. Jactel, E.S. Gritti, L. Drössler, D.I. Forrester, W.L. Mason, X. Morin, H. Pretzsch, B. Castagneyrol, Positive biodiversity-productivity relationships in forests: climate matters. *Biology Letters* 14: doi: 10.1098/rsbl.2017.0747 (2018).